THE CONTRIBUTIONS TO BOTANY OF JULIUS VON SACHS[1]

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Director Moore has very wisely divided the programme into three epochs,—Plant Physiology as Sachs Found It, The Contributions of Sachs to Plant Physiology, and Progress in Plant Physiology since Sachs. By this plan an opportunity is given the several speakers of presenting to their listeners a true perspective of the field under consideration, and of the position and influence therein of Sachs, its central figure. The first epoch we have had already passed before us, and I feel certain all have been impressed with the slow advance of physiology and of botany until approximately the middle of the nineteenth century, when, with new methods and directive thought so essential to real progress, a new era was ushered in. In this era Julius von Sachs was to play a most important rôle.

In presenting the contributions which Sachs has made, I feel that full justice cannot be done him should I confine my remarks strictly to physiology. One of his most far-reaching and lasting contributions was the masterly manner in which he coördinated the several fields of botany, and made the *functional* plant the unit of interest. This he did in his 'Lehrbuch,' first edition, 1868.

The status of botany, particularly in America and England, at that period was deplorable. The few bold spirits that ventured into the botanic field were compelled to make their way to Germany to sit as disciples at the feet of the great masters,—De Bary, Sachs, Strasburger, etc., successors or contemporaries of Schleiden, von Mohl and Hofmeister. To this galaxy of investigators, largely in the period from 1840 to 1880, we owe the most distinctive discoveries and advances in the history of botany, and to the genius of Sachs, the organization of these into a new and virile botany. When I seem to digress from the more limited subject assigned me and speak of the contributions that Sachs

[1] A paper read at the celebration held at the Missouri Botanical Garden, December 27, 1931, in honor of the one-hundredth anniversary of the birth of Julius Sachs.

made to the field of botany as a whole, I do so to emphasize the part the physiology under his leadership has played in it, and the masterful manner in which he welded the heterogeneous fragments of independent research into a real science of botany with all its branches definitely interrelated. In other words, he gave us for the first time a text-book in which the plant as a *functional machine* is lucidly and accurately brought before the student. Furthermore, to him, more than to any other contributor to the field of botany, do we owe the deep significance of the physiological division of labor in the interpretation of anatomic and morphologic structure.

For a proper appreciation of the conditions then (1868) prevailing in the field of botany, and the influence of Sachs in the molding of future progress, I cannot do better than to have former students of Sachs, men with whom a number of us have or had personal acquaintance, speak to us with their accustomed accuracy and freshness.

Farlow, in his presidential address before the Botanical Society, Cleveland, 1913, says:

> "In the laboratory [De Bary's], I noticed that the students seemed to refer frequently to a book of which I had never seen a copy or even heard. The book was Sachs's 'Lehrbuch,' second edition, 1870. I bought the book and was perfectly amazed. I had never dreamed that botany covered so large a field. The 'Lehrbuch' was an admirable summary of what was known of all departments of botany up to that date, well written and excellently illustrated. The fourth edition, which appeared while I was in Strassburg, was still better. On looking at the second edition a number of years later, I noticed what seemed to be a curious omission. No mention whatever was made of bacteria. In the fourth edition they are mentioned under *Schizomycetes*. The absence of reference to bacteria in the earlier edition, however, was not an omission. There were no bacteria until Cohn published his 'Untersuchungen über Bacterien' in 1872. The fact that forty years ago Sachs had never heard of bacteria, while to-day life has almost become a burden, one hears so much about them, is a striking instance of the rapidity of development of a subject having a practical as well as a theoretical value. I know no single book which has had so great an influence in shaping the course of modern botany as Sachs's 'Lehrbuch.' It may be that the facts there given were generally known in Germany, but they were not known in other countries. On returning home by way of England in 1874, I showed my copy of Sachs to several English botanists and it was evident that it was quite new to them. It was certainly unknown in America. If imitation is the sincerest flattery, the value of Sachs's 'Lehrbuch' was quickly recognized, for, using it as a model or basis, there soon appeared a large number of really excellent textbooks in various languages in which one recognized Sachs translated, Sachs con-

densed, Sachs diluted, Sachs trimmed to suit local demands. Publishers, were they capable of gratitude, would have erected a monument to Sachs's memory long ago. Draughtsmen, on the other hand, had little reason to bless his memory. Even now we can hardly open a new text-book without seeing the inevitable 'after Sachs.' "

From this brief extract you will note the status of botany in America in 1870. Let us next turn to England and hear in turn from Vines, Scott, and Bower an expression of the condition of botany in that country in the middle of the decade, and an appreciation of Sachs as lecturer and teacher, and of his great influence in molding and directing a new and lasting trend in botanic teaching and investigation,—a trend that has gained in impetus with a younger and better-trained generation all too frequently innocently ignorant, I am sorry to say, of a debt it owes to him to whom we this day in gratitude pay homage and tribute.

Quoting from Vines:

"In 1876 I had been appointed an Assistant Tutor at Christ's College, Cambridge, for the benefit of the increasing number of the undergraduates who were reading Natural Science, and had begun to lecture there on Botany, though I had no means for carrying on any practical work. . .

"It seemed to me, therefore, essential to equip myself further for future work by spending what time I could spare in some well-known laboratory. As such equipment was quite unobtainable in Britain, my thoughts turned naturally to Germany. Then arose the question of to which laboratory I should visit. At that time the best known of the German botanists, other than systematists, was Hofmeister, though his doctrine of 'alternation of generations' was still regarded with some suspicion by those of the more orthodox British botanists who knew anything about it; had he been still at work, I should probably have gone to him at Tübingen, but he had quite recently died. Considering that the greater part of my botanical lore had been derived from his immortal *Lehrbuch* (3rd ed. 1874), I had no hesitation in deciding that I must go to Julius Sachs at Würzburg, who was then at the zenith of his activity and fame, and whose laboratory was renowned for its physiological work. Having obtained leave of absence for the Easter Term from the College authorities, and armed with an introduction from Mr. Thiselton-Dyer, I accordingly set out for Würzburg in March, 1877. . .

"On beginning work in the laboratory, I found myself to be the only advanced student, so that I had the great advantage of the undivided attention of the Professor, which I gratefully acknowledge was ungrudgingly bestowed. The special subject of study suggested to me was that of growth, especially in its relation to light, and Sachs placed at my disposal and demonstrated to me all the available apparatus for measurement. Such was my first introduction to practical plant-physiology.

"Naturally I saw a good deal of the Professor in those early days, and an acquaintanceship developed into an intimacy which continued unbroken until his death in 1897. I often accompanied him for a stroll round the Botanic Garden

or in the shady avenues of the town, when he won my admiration by his remarkable conversational gift, discoursing of many things, not always botanical by any means, but ranging widely to include such topics as the philosophy of Herbert Spencer or the works of Lecky. . .

"He was then engaged upon his experiments, by the lithium-method, on the rate of the transpiration-current, in which I occasionally helped him and had the opportunity of observing the precision and skill with which he devised and carried them out. . .

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"Accordingly I returned to Würzburg in April, and found the laboratory much as I had left it three years before. But the 'Assistant' was now Dr. Goebel (in after years Professor of Botany at Munich). . .

"Professor Sachs was as friendly and energetic as ever, though I did not see so much of him as in 1877, for he was engaged not so much in experimental work as in the preparation of his remarkable papers on 'Stoff und Form der Pflanzenorgane.'

"I did not, on this occasion, undertake any definite piece of work, but continued the investigation of the chemical composition of aleurone on which I had been engaged off and on for some time, in which the Professor took a lively interest as it was a subject to which he had not devoted much attention. . .

"But the outstanding feature of the Semester was the Professor's course of demonstration-lectures on plant-physiology. The lectures were given on Saturday mornings, and each lasted for about two hours. Here Sachs was at his very best, inspired by enthusiasm for his subject which he did not fail to communicate to his audience. The eloquent speech; the pictorial illustration, generally by means of large sheets of white paper and a stick of charcoal instead of black-board and chalk; the manipulative dexterity; all these combined to rivet attention. . .

"Such is my story, but it would be incomplete were I to conclude without some moral reflections. The first and most obvious is—how simple, we should now call them inadequate, were the means with which the great advances in botanical science, between 1840 and 1880, were achieved in Germany! Clearly great epoch-making discoveries do not depend upon huge superlatively equipped laboratories; it is the man, not the mechanism, that counts. The next takes the form of the question—was it worth while to go to Germany to study? My answer is a strong affirmative. Brief and fragmentary as were my studies there, I recognise how great was their advantage to me, and I do not forget the debt of gratitude that I owe to the Professors who so kindly received and helped me. If the enquiry be pressed further—what was it that I gained? my answer is that I gained, not so much actual knowledge as what, for lack of a better term, I must call inspiration, the right point of view; in fact, a sort of botanical 'confirmation' at the hands of the pontiffs of the science. To make my meaning clear, I may explain that though I had read much of what there was to read on plant physiology (it was relatively little in 1877!), I had had no opportunity of comparing notes with another plant-physiologist until I went to Sachs, the fountain-head of so much of the knowledge which I had laboriously gleaned from books. His expositions of his own work, and his criticisms on the works of others, including my own, were a liberal education. I sought and found in Germany what was unobtainable in my own country."

Ten years following the experiences related by Farlow we find Scott (1880–82), upon the advice and support of Thiselton-Dyer and Vines, a student in the laboratory at Würzburg. He tells us:

> "At that time, Sachs had a high reputation in England, owing, in a great degree, to his famous Text-book, of which an English edition, translated by Bennett and Thiselton-Dyer, had already appeared in 1875. This had a marked influence on the progress of Botany in England. . .
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> "Sachs was the best lecturer I ever heard. Hard work at German, before starting from England, had prepared me to understand what I heard without much effort. The lectures were extraordinarily clear, interesting, and sometimes amusing. . .
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> "The brilliancy of Sachs's lectures was enhanced by the beauty of the sketches which he made to illustrate them. Usually these were on the blackboard, but when any specially elaborate structure was to be shown, a sheet of cartridge-paper was brought in, and Sachs made, before our eyes, a finished chalk drawing in colours—truly a wonderful performance. Later in the season Sachs started his physiology lectures, given on Saturdays. In this case, as experiments had to be demonstrated, two hours (actually one and three quarters) were allowed. Though I was never attracted to physiology, it was a great experience to witness these expositions by the greatest plant-physiologist of his time. . .
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> "Late in July, as the result of a conference with Sachs and Goebel, I decided to work for the Ph.D. At that time the subject proposed for my dissertation was the relation between leaf and branch. . .
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> "On returning to Würzburg after the long vacation, I found that Sachs had changed his mind; he no longer thought the morphological subject suitable. Such questions, he said, were not so much thought of in England as in Germany. I had never taken much to the plan myself, and was relieved when Sachs advised me to transfer my energies to a purely anatomical investigation—the development of articulated laticiferous vessels. This eventually formed the subject of my dissertation.
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> "At that time the development of laticiferous tubes in general was not so well understood as it is now; in particular, the origin of the articulated type by cell-fusion was not finally established. This was the problem which I was to help in solving."

We have heard from Farlow, a student of cryptogamic botany; from Vines, a student of plant physiology; from Scott, a student of paleobotany; and, finally, we shall hear from Bower, a student of morphologic botany, whose noteworthy contributions in that field no doubt have been influenced by his contact with Sachs. Bower says:

> "Within a few years of Hofmeister's 'Vergleichende Untersuchungen' (1851) came the 'Origin of Species' (1859). It then appeared as though a theory of evolution had merely to adopt the results already demonstrated by him. After events so stirring we need not be surprised that a pause should follow. It took time for men to realise the bearings of the new views, and still more to convert them into action. Botanically little change appeared immediately in Britain;

but within a decade an event happened in Germany which was to produce far-reaching results. It was the publication of the *Text-book* by Sachs.

"That work was written with consummate judgment, and illustrated with all the skill of a trained draftsman, who was also a keen observer. Sachs was, I believe, the son of a wood-cut artist, and had been himself trained as such. But beyond his keen vision and artistic touch, he possessed also a philosophical outlook combined with keen receptivity. These faculties made him the best possible exponent of the results of those, such as Hofmeister, whose powers of exposition were less than his own. Little wonder that the *Text-book*, which embodied not only their results but also a vast extent of Sachs' own observations, morphological and physiological, had a phenomenal success. The first English edition published in 1875 was based upon the third and fourth German editions, and it fell into my hands at once on its appearance. It came as a revelation to the group of enthusiasts beginning to gather round Vines at Cambridge, and supplied the text upon which much of our work was based. We felt then that we were daily seeing things not, it was true, new to science, but at least observed for the first time in Britain. Some of us, however, naturally looked further to the living source; and when Vines went to Würzburg in 1877, though still an undergraduate I joined him for some weeks in the summer, to sit at the feet of Sachs himself. .

"Looking back upon this period of preparation, there is no doubt that it was necessary at the time that some of us should become personally acquainted with German laboratories and methods. Going to foreign schools was the readiest way of making up that backwardness which had resulted from the academic apathy of a generation of the teaching botanists of Britain, and from their failure to keep pace with those advances in observation and laboratory technique which had grown up on the continent. . .

"It is for those who direct the progress of the teaching of the science to take care that they shall not, by allowing too early specialisation along applied channels, send out specialists too quickly and imperfectly qualified. But the more grave risk is that they should allow the central institutions to lose again their hold upon the broad stream of pure science, as their predecessors did at the middle of the last century, by over-concentration upon special requirements."

From the extracts that I have read, it is very evident that the contributions of Schleiden, von Mohl, Hofmeister, De Bary, Naegeli, Sachs, and others, made during the middle decades (1840–1880) of the nineteenth century, and which marks that period the most notable in the history of botany, had little affected the trend of botany in America or England. It was the publication of Sachs' 'Lehrbuch' in 1868, and especially the translation of a later edition into English, that proved the most potent factor in the development of botany in English-speaking countries.

The 'Lehrbuch' owed its unprecedented popularity and success to: (1) the fact that in it for the first time the widely scattered and, in many instances uncorrelated, discoveries of Sachs' predecessors and contemporaries were skillfully coördinated with his own, and

presented in a lucid, attractive style, and illustrated with figures that to this day are unsurpassed; to (2) the plan well-nigh faultless in conception and execution, in which the well-balanced treatment of the subject matter is interwoven with theories, critique, suggestive problems, and prospective lines of research; and finally, to (3) the revolutionary, I am tempted to say, treatment by which the whole of botany from cell through tissues, taxonomy, morphology, anatomy, ontogeny, and phylogeny, and the origin of species through the Doctrine of Descent, receive thoughtful consideration and masterful coördination. Throughout the book one is impressed with the persistence with which a single motive, namely, *function*, pervades and dominates the whole, and reveals to the thoughtful reader the inner workings of a great mind. In fact that seemed to have been his aim and endeavor, for we read in the preface of his Lectures as follows,—"It is not only the right but also the duty of anyone who lectures, however, to place in the foreground his own mode of viewing the matter; the audience wish to know and should know how the science as a whole shaped itself in the mind of the lecturer, and it's comparatively unimportant whether others think the same or otherwise."

Sachs, by placing emphasis on the significance of response, brought to the front the importance of the *protoplasm* of the cell as the responsive material possessed with innate developmental and adaptive potencies, and this point of view was in no small measure responsible for the change in the method and outlook of anatomy, morphology, and taxonomy. It is from this conception only, he maintained, that the origin and persistence of the great groups of the Plant Kingdom can be explained. In like manner it was the environment acting on the responsive protoplasm that brought on physiological division of labor, and with it, differentiation. This was in direct conflict with the phylogenetic view held by the morphologists and anatomists of his time, and, despite the strong criticisms of De Bary in his attempt to uphold the classification of tissues based on the history of development, the physiologic classification into epidermal, fibrovascular, and fundamental, all derived from meristem, prevailed.

Perhaps his deepest philosophic efforts were concentrated on

the finding of an hypothesis that should be helpful in the elucidation of differentiation and organ formation, and the effects of the environment on the same. In a series of contributions on 'Stoff und Form der Pflanzenorgane,' Sachs calls our attention to the impossibility of a formal morphology such as then prevailed, interpreting the significance of organs in any other manner than "als für sich Existirendes, unabhängig von jeder materiellen Grundlage angesehn." In his attempt to formulate a causal relationship between the development of an organ and its function, which he found impossible experimentally to demonstrate, he gave to us an hypothesis, which Loeb, writing in 1906, states is the "only scientific hypothesis of morphogenesis which we thus far possess." In this hypothesis, Sachs maintains that the only adequate explanation for the formation of new organs, of flowers, or of the regenerative processes must be sought in plastic materials, as yet unknown, and produced in the living protoplasm. These "formative stuffs" present in extreme small quantity, on reaching an organ, direct its growth and development in a specific manner. I need not proceed further along this line for I believe it perfectly evident that our modern conceptions of "growth-promoting," "growth-inhibiting," auxamones, yes, even hormones, are rooted in this hypothesis.

In like manner the developmental process proceeding from the egg finds here its only explanation. It is interesting to note the parallelism of expression used by Wilson in the last edition of his 'The Cell in Development and Heredity,' and by Sachs more than fifty years previously. Wilson says:

> "That a single cell can carry the total heritage of the complex adult, that it can in the course of a few days or weeks give rise to a mollusc or a man, is one of the marvels of nature. In attempting to attack the problems here involved we must from the outset hold fast to the fact that the specific formative energy of the germ is not impressed upon it from without, but is somehow determined by an internal organization, inherent in the egg and handed on intact from one generation to another by cell-division. Precisely what this organization is we do not know. We do know that it is a heritage from the past somehow perpetuated by cell-division, and that development is only a further extension of processes that have been going on since life began."

I follow, quoting from Sachs:

> "So wenig wie die ungeschlechtliche Fortpflanzung ist auch die sexuelle dazu berufen, im strengsten Sinn des Wortes einen neuen Organismus zu produziren;

die Elemente, aus denen dieser entsteht, sind selbst nur Produkte der embryonalen Substanz einer früheren Pflanze und schliesslich können wir sagen: *das was sich seit dem Beginn des organischen Lebens auf der Erde kontinuirlich immerfort in dem ewigen Wechsel aller Gestaltungen, in dem beständigen Wechsel von Leben und Tod lebendig erhalten und sich immerfort regenerirt hat, das ist die embryonale Substanz der Vegetationspunkte, die in bestimmten Fällen sich in männliche und weibliche differenzirt, um sich dann wieder zu vereinigen.* In diesen winzig kleinen Stoffmassen hat sich das organische Leben in dem langwierigen Verlauf der geologischen Epochen beständig selbst erhalten; diejenigen Thiele der Pflanzen, welche sich dem Auge unmittelbar darbieten, die ausgewachsenen Wurzeln, Sprossachsen, Blätter, die Holzmassen u. s. w., dies alles sind Produkte jener embryonalen Substanz, die sich beständig regenerirt, während diese ihre Produkte zwar an Masse millionenfach sie überwiegen, aber keiner Regeneration fähig sind; sie sind es nicht, in denen sich die Kontinuität des organischen Lebens erhält, aber sie sind es, die durch ihre gemeinsame Arbeit den Assimilationsprozess und den Stoffwechsel hervorrufen und ein sehr kleines Quantum der Substanz, die sie zu ihrem Wachsthum nicht selbst verbrauchen, wird zur Ernährung der embryonalen Substanz der Vegetationspunkte und Sexualzellen benutzt."

The two quotations taken from authorities separated by two generations in time show how well Sachs had conceived and developed these problems so fresh and fundamental to biologic thought of to-day.

Further, it is of interest to note that in the above quotation we find the idea of the continuity of the embryonic substance beautifully and unmistakably expressed three years before Weismann gave to us 'Die Kontinuität des Keimplasmas,' destined to exert such a tremendous influence on the biology of the latter part of the nineteenth century.

Continuing along the line of his studies on embryonic tissue, we find in his 'Ueber Wachsthumsperioden und Bildungsreize' a mass of material worthy of the deepest reflection by present-day physiologists. Time and space permit me to cite only two paragraphs, which, however, seem to me to express the key-note to effective physiologic experimentation with plants:

"Durch den in den Pflanze thätigen Gestaltungstrieb wird jedes sich entwickelnde und wachsende Organ, selbst jeder Theil eines solchen, in seiner äusseren Form und seiner inneren Struktur fortschreitend verändert: das Organ ist heute nicht mehr dasselbe Ding wie gestern und wird morgen wieder ein Ding mit anderen Eigenschaften sein, selbst wenn man dies an der äusseren Form und der mikroskopischen Struktur nicht wahrnimmt.

"Wird nun das sich entwickelnde, wachsende Organ von äusseren Einwirkungen betroffen, welche die Art seines Wachsthums verändern, so muss diese Reaction verschieden ausfallen, je nachdem die gleiche äussere Einwirkung das wachsende Organ gestern, heute oder morgen trifft."

I feel confident that the discordant results with the use of similar organisms now so frequently reported may be greatly lessened through a more conscientious study of the principles suggested in the above quotation. The physiological phase of development at the time of experimentation, and a more detailed attention to the environmental factors to which the plant is exposed preceding the experiment, should receive the same serious attention now as then.

Proceeding from these philosophic aspects of the meristem or growing tip, I may pass to a brief consideration of his views on cell activity and cell relation. Because of his strong bias, and consistent with his view concerning the developmental process, Sachs took the position very effectively described by Hertwig as follows:

> "Although from the point of view of the morphologist it has become more and more imperative to regard the cell as the unit of the higher organism, still, from the physiological point of view, the higher organisms must be regarded as masses of material of structural parts subordinate in function to the whole, and displaying only a limited division of capacities. And so the cell theory, according to which the cell was exalted unduly as the unit of life, the center of life, the elementary organism, must take limitation and correction from these wider views."

With the emphasis placed on the organism rather than on the cell, Sachs clearly saw that the complex of tissue cells in the plant, encased as they are in cellulose walls, must have some provision by which the whole is organized into an interacting community and suspected protoplasmic connections long before their actual demonstration. In a series of articles under the general head 'Beziehungungen zwischen Zellbildung und Wachsthum,' he makes clear his ideas on the relation between growth and cell-division, and insists that growth is primary and cell-division secondary. Here he also develops his principles of cell-division as (1) cells divide into equal parts, and (2) each new plane of division intersects at right angles the previous one, subsequently elaborated by Hertwig. His elaborate studies on the geometrical relations of cleavage-planes in growing plant tissues which are either anticlinal or periclinal, received much attention and are not without interest to-day. He was the first to call our attention to the relation between size of cell and size of organism.

I shall next pass to the consideration of the more important

contributions in experimental physiology contributed by Sachs, and on which the superstructure of present-day physiology was built. The task of presenting the gist of one hundred papers is not an easy one, and time does not permit of great detail. I shall therefore confine myself to brief remarks concerning those researches that, in my opinion, were most important in the development of experimental physiology of which he is the recognized founder, and as my guide I shall, in general, follow the headings as given in his 'Gesammelte Abhandlungen.'

In the first section, "Ueber Wärmewirkungen an Pflanzen," we find several contributions of present-day interest. His studies on crystal formation in the freezing of plant tissue corrected false conclusions that had been previously held, but he was unfortunate in his explanation of the cause of death. His studies on "Vorübergehende Starre-Zustände" (1863) furnished us new and detailed information regarding heat and cold rigor, and gave us the terms phototonus and thermotonus. Here as elsewhere in his discussions on response he says that "irritability both in the vegetable and animal kingdom must in the main be full of purpose." The use of the word purpose has misled many botanists. They not infrequently have accused him of having marked teleological views. This, I believe to be wrong, and a careful reading of his contributions will, I think, correct such an impression. A single quotation from Sachs will make this clear:—"But the fact that, formerly, purpose in the mechanism of organisms was referred to causes other than now, is no reason for robbing our language of a pregnant term. By the expression, This or That mechanism has a purpose in an organism, one understands really nothing more than that this contributes to the ability of the organism to exist." In his studies on germination as affected by temperature, and of maximal temperatures on vegetation, he presents a wealth of information obtained by experimental methods which was new and stimulating then, and to which we even now return. In these papers the terms minimum, optimum, and maximum as the cardinal points were for the first time employed, and the effects of supra temperatures on the several cell functions, for example, turgor and permeability, permanently established. Mention should also be made here of the effects of

minimal temperatures required for chlorophyll formation, even in the gymnosperms where ordinarily chlorophyll forms in the dark.

The second section, "Ueber Licht-Wirkungen an Pflanzen," deals with the transmission of light through plant structures, and brings into use the diaphanoscope revealing the change in the transmitted light due to chlorophyll absorption; with the morphogenic influence of light on the growth, unfolding, etc., of the several plant organs; with the action of colored lights on plants in which his chief object was to determine experimentally the similarity or dissimilarity between the action of different lights on the chlorophyll formation and gas evolution in plants and on silver chloride. In the same paper he investigated chlorophyll formation and tropic response in blue and orange light,—double-walled bell jars—and the disintegrating action of this light on a chlorophyll solution.

The third section, "Ueber Chlorophyll und Assimilation," brings to us a series of papers generally conceded as among the most stimulating contributions to physiology. Here he demonstrates that starch is the first distinctly recognizable product in photosynthesis, and related its formation to the action of light on chlorophyll. Further, he enters into a quantitative study of the product, gravimetrically and with the still much-used iodine test. With the use of tin-foil partially covering the illuminated leaf, he shows the dependence of the product on light, and that it is strictly localized; he shows its decrease under less intensive insolation, its disappearance in the dark, and surmises that it is converted into sugar for translocation.

The fourth section, "Ueber Bewegungen des Wassers in Pflanzen," considers among other things, the experimental evidence on which he based his imbibitional theory. Unfortunately the theory itself has been found wanting, though it must be admitted that many of the details that Sachs gave to us are used in the newer and more satisfactory theories of to-day. To our knowledge of transpiration he added a great deal, and started lines of investigation which are at present still receiving well-deserved attention. His experiments on the saturation capacities of soils of different chemical and physical composition, and the amount of water that a

root system is capable of absorbing, were fundamental in their conception and still offer problems in modern physiology. He successfully correlated transpiration with soil moisture, temperature, acid and alkaline reaction, etc., and insisted that it must be considered with other vital processes of the plant. He recognized the difference between cuticular and stomatal transpiration, and attributed the much greater quantity of the latter to the intercellular spaces in the mesophyll with which the stomates communicate. He supplemented the views of Schwendener and suggested that the turgor phenomena are traceable to the osmotically active substances produced by the chloroplastids in the guard cells, and made the stomates the path of gaseous interchange. He held untenable the view that root-pressure is a factor in the movement of water, but attributed to the suction force of transpiration very much the same office as do the accepted theories of to-day.

In the fifth section, "Ueber das Verhalten der Baustoffe bei dem Wachsthum der Pflanzenorgane," he follows the transformation of the oil in oily seeds into starch and stated that in all probability it was translocated as a sugar. In a series of beautiful figures and comprehensive tables he indicates the presence or absence of oil, starch, or albumin, and thus strengthens his physiologic interpretation of the tissue systems. Following this are four contributions on the germination of the bean, grasses, date, and onion, all worked out with the same care and laying the foundation for all subsequent studies. The last paper in the series concerns itself with the "acid, alkaline, or neutral reaction of living cell saps,"—a title that sounds extremely modern.

The sixth section, "Ueber das Wachsthum von Sprossen und Wurzeln," brings to us his epoch-making studies on growth in which temperature and light are considered in their influence on daily periodicity in growth. Here, too, are given us the observations that brought to our attention for the first time that distribution in the growth phase that he named the Grand Period of Growth; here he gave to us the auxanometer; described and defined nutation in contrast to circumnutation; showed the effect of the environment—air, water, or soil—on the growth of main and lateral roots and of the angle of the latter to the main root, and the distribution of growth in the responsive processes to

gravity, etc. Through his simple demonstration of the growth of a root into mercury, he silenced the contention generally held that the curvature is a mechanical process due to the action of gravity on the root mass, and added another convincing point to his contention that all responses are vital.

In the seventh section, "Ueber die Tropismen als Reiz wirkungen," we find him developing his vital theory to irritability. Here we have the first and most conclusive evidence ever offered of the effect of age or physiologic phase, and of the effects of previous exposure, on the reaction of the plant organ. He calls to our attention the difference in response to the same stimulus of the main and the lateral roots, and introduces the terms orthotropism and plagiotropism. He demonstrates the response of the root to differences in moisture, hydrotropism, and gives us his simple but effective sieve method. In the response of plant organs to light, he lays stress on the importance of the direction of the rays, invents and illustrates the use of the klinostat in investigations of this sort. He calls attention to the difference between growth response and turgor response as illustrated in pulvini.

I feel that I must not close this paper without some reference to the cordial interest that Sachs at all times maintained toward the young men in his laboratory, and his deep conviction that the teaching process is one worthy of serious attention and concern. The following story told me by Professor Fritz Noll only a year after Sachs' death, I am sure, will be of interest to all: Noll had been appointed assistant to Sachs and was entering with fear and trepidation the lecture room for his first lecture. He was met by Sachs who told him that he would find the door leading from his study into the lecture room slightly ajar. This, he said, was not with an eaves-dropping intent, but rather for the purpose of following his lecture while at work, thus to be able to give suggestions for possible improvement. He further requested that Noll call at his (Sachs') office immediately following the lecture. I am sure that all of you can imagine the strain on a young assistant when the master listens intently to the efforts of the amateur. Noll told me that the training there received was of the very best. Always kind and considerate, Sachs would commend Noll on the

manner of presentation of one phase of the subject, but would show him, with kindly consideration to his feelings, how the presentation of another phase could have been much improved.

Thus I have briefly reviewed the more important contributions to botany in general, and plant physiology in particular, made by Sachs, the one-hundredth anniversary of whose birth we are here met to celebrate. The number would be greatly increased had I included the many and noteworthy contributions made in his laboratory by such students as Goebel, De Vries, Pfeffer, Vines, Bower, etc. Truly, I think, can the criterion which he used in measuring worthiness for consideration in his History of Botany, be applied to him,—"I have, therefore, singled out those men as the true heroes of our story who not only established new facts, but gave birth to fruitful thoughts and made a speculative use of empirical material."

Explanation of Plate

PLATE 2

Two of three original Bell jars for light experiments made for and used by Sachs at Bonn. Prof. Max Koernicke holding a round marble plate, original root-etching experiment.

Photo by Prof. F. E. Lloyd.